

# POLLEN LOADS OF HONEY POSSUMS (*TARSIPES SPENSERAE*) AND NONFLYING MAMMAL POLLINATION IN SOUTHWESTERN AUSTRALIA<sup>1</sup>

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## ABSTRACT

Pollen loads were analyzed from 30 honey possums in the Albany region of southwestern Australia. The pollen of *Banksia attenuata* was the major component of the pollen loads followed by *Adenanthos cuneata* and *Banksia coccinea*. The data from pollen loads and flower-head morphometrics indicate that *Tarsipes* is the primary pollinator of *Banksia attenuata*, and not birds as might be surmised from other characteristics. *Tarsipes* also visits typically bird-pollinated plants such as *Banksia coccinea* and *Adenanthos cuneata*, but little or no pollination would be expected from such visitation. The lack of distinct flowering seasonality in the southwestern Australian flora is correlated with the presence of a high percentage of long-lived, resident pollinators such as birds and nonflying mammals. A number of plant genera are mentioned which show possible adaptations for pollination by nonflying mammals. Several groups of small mammals which might play a role in pollination are also discussed.

Pollination by nonflying mammals has been the subject of renewed interest in recent years (Rourke & Wiens, 1977; Wiens & Rourke, 1978; Sussman & Raven, 1978; Holm, 1978; Carpenter, 1978; Hopper, unpubl. man.). There is, however, a dearth of definitive and, especially, quantitative data on the subject. Any general analysis of pollination by nonflying mammals must consider the unusual biota of southwestern Australia. This region has the highest concentration of plants presumed to be pollinated by these animals. One of the most unusual mammals in southwestern Australia (if not the world!) is the mouselike marsupial honey possum (*Tarsipes spenserae*). The incredible adaptations of this animal to a presumed diet of nectar (and pollen?) were summarized by Rourke & Wiens (1977) and Holm (1978). Various aspects of its biology were discussed by Vose (1972, 1973) from observations on animals in captivity. It is widely assumed, especially by Australian biologists, that the honey possum is a coadapted pollinator of various plants in the region, but we are unaware of any published information to corroborate these assumptions. The primary object of the study, therefore, was to determine if captured feral honey possums carried pollen loads, and if such pollen is positioned to effect regular pollination of those flowers involved.

## METHODS

Honey possums and meliphagid birds (honey eaters) were captured during three successive days and nights (Dec. 1–3, 1978) at two study sites (Umagallee and Kaylah) on the William Dunlop farm along Highway 1, approximately 45

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km east of Albany, Western Australia. The vegetation of this area is composed of dense sclerophyllous shrubs often dominated by *Banksia* (and the ubiquitous Australian flies!). Locally the area is known as heathland or quangen and is part of the southwestern floral province of Australia, which is characterized by an exceptionally high diversity of species.

Honey possums were live-trapped in pits 40–50 cm deep. The pits were lined with smooth plastic drainpipe (7.5 cm in diameter) to prevent trapped animals from escaping up the sides. The traps were checked early each morning and the captured animals tested for pollen on the snout and forehead and released. Honey eaters were trapped in mist nets, checked for pollen, and also released.

The presence of pollen was determined by rubbing gelatin blocks approximately 5 mm<sup>2</sup> and 2 mm thick through the hair or feathers of the respective animal (Beattie, 1971). The blocks were then placed on a warmed slide, melted, and spread under a cover glass 22 mm<sup>2</sup>. Such slides are prepared in seconds and the pollen adhering to the blocks is readily trapped and stained (basic fuchsin is a component). When cooled, the preparation is essentially permanent. Identification of the pollen, where possible, was accomplished by comparison to samples taken from flowers collected on the study sites.

Freshly defecated feces were obtained from two newly captured *Tarsipes* and similarly sampled for pollen content, except that the gelatin block was simply touched directly to the surface of the soft fecal mass. The number of pollen grains on the slides was determined by systematic scanning of the gelatin layer under a compound microscope. In fecal samples, however, the pollen grains could not be counted precisely because of the large numbers involved.

## RESULTS

Thirty honey possums were captured during the study. All carried pollen on their snout and forehead, however, the quantity varied widely (Table 1). The pollen loads were derived from at least 12 species of flowering plants, but the pollen of *Banksia attenuata* was clearly the most common. The high number of *Adenanthos cuneata* grains was due primarily to a single sample (No. 10) which accounted for 536 of the 854 total and distorted both the total and the mean for this species. A more accurate indication of the importance of this species in terms of pollen load composition is evident from the mode, which is approximately four times higher for *B. attenuata*. The pollen of *Callistemon speciosus* and *Banksia coccinea* was present in approximately equal proportions. The remaining pollen represents a number of unidentified species not observed in the immediate areas of the study sites.

Only three species of flower birds (Meliphagidae) were captured, but their pollen loads were much larger than on *Tarsipes*. Presumably this is because *Tarsipes* frequently removes pollen by grooming (Vose, 1972). Birds may occasionally preen themselves, but they were effectively immobilized in the mist nets whereas the honey possums captured in pit traps had freedom of movement for grooming. Also the pollen loads on the honey eaters was much less diverse and composed almost entirely of pollen from *Banksia coccinea* and *Adenanthos cuneata*; no pollen of *B. attenuata* was present.

The fecal samples of *Tarsipes* were of special interest because they were



TABLE 1. Continued.

Animal	Sam- ple No.	No. of Pollen Grains											
		<i>Bank- sia atten- uata</i>	<i>Banksia coccinea</i>	<i>Banksia grandis</i>	<i>Ade- nanthos cuneata</i>	<i>Calli- stemon speciosa</i>	<i>Hakea sp.</i>	<i>Melaleuca thymoides</i>	<i>Petro- phile longi- flora</i>	Sp. A.	Sp. B.	Sp. C.	Sp. D.
<i>Tarsipes spenserae</i>	27	149	9	5	53								
<i>Tarsipes spenserae</i>	28	1			22								
<i>Tarsipes spenserae</i>	29	53	4		2								
<i>Tarsipes spenserae</i>	30	38	3		4								
Total		974	191	11	854	19			3	318	34	2	
Mean		32	6	0.4	28	0.6			0.1	11	1	0.06	
Mode		11	1	0	3	0			0	0	0	0	
<i>Acanthorhynchus superciliosus</i> <sup>a</sup>	1				100%								
<i>Acanthorhynchus superciliosus</i> <sup>a</sup>	2		<0.01%		73%		<0.01%	<0.01%					26%
<i>Phylidonyris novae hollandiae</i> <sup>a</sup>	3		71%		29%								
<i>Phylidonyris novae hollandiae</i> <sup>a</sup>	4		83%		17%								
<i>Phylidonyris nigra</i> <sup>a</sup>	5		75%		25%								
<i>Phylidonyris nigra</i> <sup>a</sup>	6		62%		33%		0.02%	0.03%					

<sup>a</sup> Because of the excessively large number of pollen grains in most of the honey eater samples (well into the thousands), all the grains were not counted and the data are expressed as percentages.

composed of almost solid pollen residue. The freshly defecated feces are a black, "mushy," amorphous mass and in no way resemble the hard fecal pellets typical of small mammals. The pollen was interspersed in a black substance giving the feces its characteristic color, and also contained numerous unidentified opaque granules (sand grains?). Because the feces were obtained immediately upon defecation, they were presumably uncontaminated.

#### DISCUSSION

The high percentage of pollen from *Banksia attenuata* present in the pollen loads suggests that flowers of this plant received the highest frequency of visitation by *Tarsipes* during the study period. The high density of *B. attenuata* pollen in the feces also supports this contention. Initially, this seems surprising because *B. attenuata* is a small- to medium-sized tree (up to 14 meters) with highly visible and easily accessible terminal spikes of yellow flowers (Holliday & Watton, 1975). These characteristics strongly suggest bird pollination. Several Meliphagidae (honey eaters) are known to visit the spikes, e.g., the yellow-throated miner (Morcombe, 1968), the New Holland honey eater, western spinebill, white-cheeked honey eater, and no doubt others. The pistil of *B. attenuata*, however, is only 11 mm high and many flower birds in western Australia have bills twice that length. Thus, if birds pollinate *B. attenuata*, it must be effected largely by pollen transferred from the bill. This seems unlikely since the surface of the bill is poorly adapted to hold pollen, but pollen was observed by Burbidge et al. (1979) on the beak of a New Holland honey eater. Feathers of the head and breast are the commonly used medium for retaining and transferring pollen in typical bird-pollinated species. Such a situation is beautifully illustrated in a photo by Morcombe (1968: 38) for the yellow-throated miner. The bird is shown probing the flowers of *B. attenuata*, but the style reaches no farther than about a third of the distance up the beak.

The floral morphometrics of *Banksia attenuata* are not well adapted for pollination by birds. The head of *Tarsipes*, however, does correlate with the size and shape of the flowers, especially when one considers that its brushed tongue is extensible up to two centimeters beyond the snout (Vose, 1973). The heads of *B. attenuata* also emit a fermentedlike odor, which directly supports the idea of pollination by nonflying mammals (Rourke & Wiens, 1977). Furthermore, the odor is surprisingly similar to that described by Wiens & Rourke (1978) for South African species of *Protea* pollinated by rodents. We are unaware of any typically bird-pollinated flower which produces strong fermentedlike odors. cursory attempts to determine the time of nectar production in *B. attenuata* were equivocal, but Morcombe (1968) reports nectar production in this species is particularly abundant at night. *Tarsipes* apparently forages nocturnally and is scansorial, which further supports nonflying mammal pollination for *B. attenuata*.

If *Banksia attenuata* is pollinated primarily by *Tarsipes*, it explains the seed-set results obtained by Whelan & Burbidge (unpublished data) using enclosure experiments to exclude birds from the spikes of *B. attenuata*, *B. menziesii*, and *B. littoralis*. Seed set occurred in both *B. attenuata* and *B. littoralis*, but not in *B. menziesii*, when the spikes were enclosed in 0.5 inch hexagonal wire mesh

designed to exclude birds. The head of *Tarsipes* is approximately 11 mm wide ( $N = 2$  animals), and is thus able to penetrate such an enclosure. We predict that *B. menziesii* is primarily bird pollinated; thus the lack of seed set in this species could also be explained.

If *Banksia attenuata* is pollinated primarily by nonflying mammals, it raises the intriguing question of how the pollinators are attracted to the spikes which may be many meters above ground level (Holliday & Watton, 1975). Odor must be the primary cue, but its effectiveness so high above ground level seems dubious. Carpenter (1978) reports that *B. ericifolia* in eastern Australia (also a small tree) secretes nectar into longitudinal channels on the spikes which then drips to the ground and lower foliage, and in this way, presumably, attracts nonflying mammals to the plants. *Banksia attenuata*, however, possesses no such nectar channels and cursory observations showed no evidence of nectar secretion from the spikes to the ground. Several banksias, however, secrete nectar directly from the tips of the corolla. Unlike most banksias, the corollas of these species remain united except at the apex. The texture of the corolla in these instances is hard and smooth. Thus they would not be expected to retain nectar easily by surface tension. *Banksia lemmaniana* is an excellent example of this "nectar drip" attraction system. Species with similar corolla types include *B. caleyi*, *B. elegans*, *B. lindleyana*, and *B. sp. nov.* (George, pers. comm.). Keighry (pers. comm.) states that *B. tricuspis* also secretes nectar from the spikes, but utilizes a different method. Some of these species also have pendulous heads, which might be important in this particular system of "nectar drip" attraction.

Carpenter (1978) also suggested that the hooked style in some species of *Banksia* was an adaptation for pollination by nonflying mammals. This is almost certainly correct, but in addition many straight-styled species, such as *B. attenuata* and *B. lemmaniana*, are also probably pollinated by nonflying mammals. We estimate that perhaps 50% or more of the banksias are mammal pollinated.

The high concentration of pollen residue in the feces of *Tarsipes* indicates it is largely a pollen feeder, or that pollen (as in many bats) is at least an important element of the diet. Supporting this contention is the fact that in several instances captive *Tarsipes* primarily licked the pollen from the styles of *Banksia attenuata* and also probed for nectar. Vose (1972) also mentioned that captive *Tarsipes* licked pollen from the flowers. The pollen mass of *B. attenuata* is peculiarly viscous, and perhaps it is coated with a nutritionally valuable lipid layer as recently mentioned by Baker & Baker (1979).

While the pollen of *Banksia attenuata* is the primary constituent of the pollen loads of *Tarsipes*, the pollen of *Banksia coccinea* and *Adenanthos cuneata* is also consistently present (Table 1). That *Tarsipes* (or any other nonflying mammal) is an effective pollinator of these latter two species, however, is highly improbable on the basis of both morphometric and attraction criteria. The pollen loads collected from the honey eaters, however, show that *B. coccinea* and *A. cuneata* pollen predominates and that pollen of *B. attenuata* is not present (Table 1). Thus, while birds certainly visit *B. attenuata*, they may not transfer pollen easily or accumulate it in their pollen loads; however, the sample size of honey eater pollen loads in this study is small and additional data are necessary for confirmation. Possibly *Tarsipes* visits typically bird-pollinated flowers primarily

for pollen. Because some pollen of these species also accumulates on the snout and forehead, nectar probing is also indicated, since licking pollen does not normally transfer pollen to the head of *Tarsipes*. The pollen in the feces, however, probably represents the feeding activities of no more than the previous 24 hours, whereas residual pollen in low concentrations might remain on the forehead and snout for considerably longer periods in spite of repeated grooming.

Many flowers in southwestern Australia are obviously visited by both birds and nonflying mammals and determining the relative effectiveness of these potential pollinators will not always be simple. The problem was also encountered by Hopper (unpubl. man.). Critical analyses of floral-pollinator morphometrics, the nature of the floral attracting cues, and behavior of the animals at the flowers will be necessary to resolve these problems.

Long-lived coadapted pollinators such as nonflying mammals and birds must have a continuous supply of nectar and pollen. These resources are provided by plants through temporal partitioning of the flowering periods in a given community. A cursory inventory of the Umagallee study site showed that *Banksia attenuata*, whose pollen predominated both the pollen loads and fecal samples of *Tarsipes*, was blooming on the study site. In addition the following species, perhaps pollinated by nonflying mammals (but not then in flower), also occurred on the study site: *Banksia dryandroides*, *B. prostrata*, *B. quercifolia*, and *B. sphaerocarpa*; *Dryandra sessilis* and *D. cf. plumosa*. Insufficient phenological data are available to determine if the flowering periods of these species overlap properly, or if the plants are present in sufficient densities to provide the continuous supply of nectar and pollen necessary to attract and maintain nonflying mammal pollinators. Species in other genera on the study site, however, may also be pollinated by nonflying mammals, e.g., *Beaufortia*, *Callistemon*, *Calothamnus*, *Conospermum*, *Eucalyptus*, *Hakea*, *Isopogon*, *Melaleuca*, *Petrophile*, *Pimela*, and *Regelia*. Monitoring the pollen loads and fecal contents at two to four week intervals for a year should elucidate the changing food resources of nonflying mammal pollinators, and a permanent marking system should indicate if local migration to new floral resources is periodically necessary. Considerable data could be obtained regarding plants putatively pollinated by nonflying mammals by noting the behavior of captive animals when presented with the flowers of various species (Vose, 1972).

Because the flora of the coastal region of southwestern Australia (the southwest province) has an apparently high percentage of bird- and nonflying mammal-pollinated flowers, distinct seasonality of blooming should be reduced so that a constant food source is available. This feature, in fact, was noted for this flora decades ago by Diels (1906). Interestingly, the distribution of *Tarsipes* is virtually restricted to this vegetative zone (Vose, 1972). *Banksia* (ca. 70 species) and *Dryandra* (ca. 80 species) are probably the most important genera involving nonflying mammal pollination, but *Eucalyptus* (ca. 450 species) needs further study in this regard. We estimate that at least half the banksias and most dryandras (probably the largest endemic west Australian genus) are pollinated by nonflying mammals. Furthermore, dryandras flower mostly during winter when fewer plants are blooming. A monthly calendar of bee plants for the coastal plain (Smith, 1969)

shows that at least one species of *Banksia*, *Dryandra*, or *Eucalyptus* is in flower each month of the year.

The extent of pollination by nonflying mammals in the rich flora of southwestern Australia is unknown. Rourke & Wiens (1977) listed 11 marsupials and 1 placental mammal which were reported to take nectar from flowers. The only data on actual pollen loads on Australian mammals are in a paper by Carpenter (1978) on *Rattus fuscipes*, the material reported here, and additional data for *Tarsipes* obtained by Hopper (unpubl. man.). Additional information of anecdotal origin is available, however, which we mention with the hope that it will stimulate further studies.

R. Young (pers. comm.) has observed *Pseudocheirus peregrinus* taking nectar from *Eucalyptus* flowers. M. Morcombe (pers. comm.) has observed *Mus mus-telloides* on the spikes of *Banksia attenuata*, and also reports that *Petaurus breviceps* takes nectar from flowers in captivity. D. Kitchener (pers. comm.) suggests that the following animals might also play a role in pollination: *Melanomys* sp.; *Ningauia timealeyi*, *N. ridei*; *Pseudomys albocinereus*, *P. occidentalis*; and *Smithopsis* sp. T. Milewski (pers. comm.) also suggests *Pseudomys* as a potential pollinator and points out that the approximately six species are habitat specific in sclerophyll shrub communities, but the factors restricting their distribution are unknown.

To our knowledge *Tarsipes* is the only nonflying mammal known to have coevolved structural and, presumably, physiological and behavioral characteristics which adapt it to a diet of nectar and pollen. Preliminary observations of liquid preserved pygmy possums (*Cercartetus concinnus*) in the Western Australia Museum suggest it also has a brushed tongue, but detailed studies are needed for confirmation. Wakefield (1963) states that the diet of pygmy possums is restricted to nectar, insects, and other arthropods; a photograph shows it foraging on the flowers of *Eucalyptus leucoxylon*.

Utilizing skins in the Western Australia Museum, the heads of some of the animals mentioned above were tested for pollen loads. Since skins are normally cleaned prior to accessioning, the chances of finding pollen would not seem high. Nevertheless, pollen tentatively identifiable as *Banksia attenuata* was found on *Smithopsis*, and pollen was also recovered from *Cercartetus*. The technique could be valuable to determine potential nonflying mammal pollinators and the plants they might visit.

The number and groups of plants adapted for pollination by nonflying mammals in southwestern Australia is largely unknown. In addition to those mentioned previously and those summarized by Rourke & Wiens (1977) from various sources, the following suggestions are offered by A. George (pers. comm.): *Bacteria* (Xanthorrhoeaceae), *Conostylis* (Haemodoraceae), those species with semi-cryptic ground flowers; *Darwinia* (Myrtaceae), a few ground-flowering species, e.g., *D. speciosa*; *Lamarchea* (Myrtaceae), a monotypic ground-flowering species; *Verticordia* (Myrtaceae), perhaps *V. cauliflorous* and *V. penicellatus*. In addition the genus *Brachysema* (Papilionaceae) has several geoflorous species that might be pollinated by nonflying mammals. *Brachysema* and a number of other genera, however, have ground-flowering species which appear to be bird



pollinated. We recognize that geoflory, per se, is not necessarily an indication of pollination by nonflying mammals.

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